COMPARATIVE MAXILLARY AND DENTARY MORPHOLOGY OF THE AUSTRALIAN DRAGONS (AGAMIDAE: SQUAMATA): A FRAMEWORK FOR FOSSIL IDENTIFICATION

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The maxilla, particularly its anterior portion, and dentary of extant Australian agamids, excluding *Cryptagama* and *Hypsilurus,* provide a framework for identification of fossil agamids. Juvenile agamids can be distinguished from adults on their pleurodont teeth relative to the first acrodont tooth, a posterior-most acrodont tooth that is the largest in the tooth row, and acrodont teeth with translucent margins. Sexual dimorphism occurs in *Ctenophorus maculatus, C. pictus* and *Tympanocryptis intima,* which have distinctly larger maxillary caniniform pleurodont teeth in males than in females. *Amphibolurus, Lophognathus, Caimanops, Chlamydosaurus* and *Diporiphora* share many features including, an angular dorsal maxillary process and reduced naris ridge. *Amphibolurus* shares most features with *Lophognathus gilberti* and *Lophognathus temporalis. Caimanops* is morphologically similar to *Chlamydosaurus*, but is smaller and *Diporiphora* is similar to *Amphibolurus nobbi,* but smaller. *Tympanocryptis* differs from *Rankinia* by its caniniform pleurodont dentition. The *Ctenophorus reticulatus* species group is closest to *Pogona*, possessing rounded maxillary and dentary acrodont dentition. *Physignathus* and *Chelosania* share more features with each other than with other Australian agamids. *Moloch* shares many features with *Tympanocryptis*, including the vertical dorsal maxillary process and angled maxillary acrodont teeth. Although *Moloch* has many derived features of the maxillae and dentary, it also has features of the more plesiomorphic *Physignathus* and *Chelosania.* ❐ *Australian, Agamidae, comparative morphology, maxilla, dentary.*

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Dragon (or agamid) lizards are a conspicuous group of Old World squamates, found in most Australian terrestrial environments. They exhibit a diversity of form and behaviour, which is paralleled only by their iguanian New World relatives. Frills, humps, beards, sails and facial ornamentation provide a range of external characters as the basis of most agamid species. However, external features are useless in identifying fossil agamids. This paper describes morphological variation in the maxilla and dentary of Australian agamid genera (except *Cryptagama* and *Hypsilurus*) as a framework for fossil identifications and phylogenetic reconstruction. Siebenrock (1895) was apparently the first to illustrate skulls of Australopapuan agamids; including *Moloch horridus*. Cogger (1961) used agamid skull morphology and morphometries to define Australian taxa with neotenic characteristics. Mitchell (1965) considered osteological data to separate *Ctenophorus maculosus* from *Tympanocryptis*. Badham (1976) provided osteological data to separate species of *Pogona*. Kent (1987) noted osteological features of *Rankinia diemensis*. Greer (1987, 1989a) described the postcranial osteology of *Ctenophorus clayi* and *Ctenophorus femoralis*. Greer (1989b) reviewed osteological knowledge of Australian agamids. Witten (1993) summarised the skeletal system of Australian agamids, noting that the general caniniform nature of agamid pleurodont dentition with specific reference to the extreme enlargement of the pleurodont dentition in *Chlamydosaurus* and *Tympanocryptis*. *Caimanops, Diporiphora, Ctenophorus pictus* and *Ctenophorus rufescens* all share equivalently large, caniniform pleurodont teeth. Examination of specimens in this study reveals some necessary modifications to earlier works: Covacevich et al., (1990, fig 1) in illustrating a series of Australian agamid maxillae and dentaries transposed captions to two figures (fig. 1g – *Caimanops amphiboluroides* = *Tympanocryptis tetraporophora*; fig. 1h – *Tympanocryptis tetraporophora* = *Caimanops amphiboluroides*; fig. 1i – *Ctenophorus caudicinctus* = *Lopognathus gilberti*; fig. 1j – *Lophognathus*

gilberti = *Ctenophorus caudicinctus*); Witten (1993: 243) noted "...*Moloch horridus* has lost the anterior pleurodont teeth...". *Moloch* specimens examined herein have 2-3 premaxillary, 3 maxillary and 3 dentary pleurodont teeth in each tooth row. Witten's (1993, fig 29.5B, C) skull drawing of *Hypsilurus boydii* represents specimens now identified as *Physignathus lesueurii* rather than *Hypsilurus boydii*.

An osteological framework for identification of modern and fossil agamids is lacking (Archer, 1978; Estes, 1985; Molnar, 1991; Molnar & Kurtz, 1997; Mackness & Hutchinson, 2000). Attempts to identify fossil agamids below family level, include Lydekker (1888) who identified *Chlamydosaurus kingii* from the eastern Darling Downs; Smith (1976) who identified *Amphibolurus* from the Naracoorte Caves, tentatively assigning them to *A. barbatus*, now *Pogona barbata*; and Covacevich et al., (1990) who identified *Physignathus* sp. and *Sulcatidens quadratus* (Fig. 1B, C), from the Oligocene-Miocene of Riversleigh, using maxillae and dentaries.

METHODS

Systematics for this study follow Cogger (2000) and Wilson & Knowles (1988) with a few modifications. Recognition of *Rankinia* follows Greer (1989b). *T. pinguicolla* was raised to species level by Smith et al. (1999) who used molecular data with little morphological and no osteological data, making it impossible to determine the comparative specimens referred to only as *T. lineata*. *T. lineata* and *T. pinguicolla* are treated as synonyms, until skins of the skeletons used in the present study can be properly identified. *Diporiphora* has been split into two groups based on maxillary pleurodont tooth count as a tool to differentiate species within this large genus. *Ctenophorus* species groups are based on external morphology (Wilson & Knowles, 1988). This allowed the greatest diversity of osteology to be analysed with at least one species within each of these species groups attained for the present study. Osteological data suggest that species groups should be combined, as in Witten (1982). However, this is reserved until a larger collection of skeletons is available.

At least one adult and one juvenile of each Australian agamid genus, except *Cryptagama*, have been examined to distinguish juveniles from adults. *Cryptagama* was not available for observation. *Hypsilurus* (Figs 8E, 9M) is illustrated but not described because it is to be included in a forthcoming review of Australian and PNG agamids. Species variation has been noted where numerous skeletal and spirit specimens are available (e.g. *Chlamydosaurus kingii*, *Physignathus lesueurii* and *Pogona barbata*). Two or more adult skulls of each monotypic genus are available, except *Caimanops* where only 1 was available. For polytypic genera the numbers of skulls available were: *Amphibolurus* (7), *Ctenophorus* (58), *Diporiphora* (14), *Hypsilurus* (5), *Lophognathus* (10), *Pogona* (13), *Rankinia* (3), *Tympanocryptis* (9).

Variations in pleurodont and aerodont tooth counts, orientation, size and shape were noted on defleshed skulls and spirit specimens. Teeth on the latter can be examined by making a small labial incision and carefully pealing the scales back with a pair of fine forceps. Morphological features referred to herein are illustrated in Fig. 4.

Specimens (Appendix 1) are deposited in the Queensland Museum (QMJ), Museum and Art Gallery of the Northern Territory (NTR), Australian Museum (AMR), Western Australian Museum (WAMR), Muséum d'Histoire Naturelle (MNHN) and University of Michigan Museum of Zoology (UMMZR).

AGAMID OSTEOLOGY AND ONTOGENY

The most diagnostic skeletal feature of agamids, and their sister taxon the chameleonids, is the acrodont dentition on maxilla and dentary (Cooper et al., 1970). This feature defines the Acrodonta (Frost & Etheridge, 1989), a group with Cretaceous ancestry (Moody, 1980). Agamids also possess anterior successional pleurodont teeth. Pleurodont teeth begin their eruption sequence with the egg tooth in the midline of the premaxilla. Throughout ontogeny pleurodont teeth are replaced by larger successors that either remain in their fixed position or are displaced by newly erupting pleurodont teeth posteriorly. In adults, eruption of the final pleurodont tooth series initiates wearing down of the tooth row. It is common to find a tooth row completely devoid of functional teeth, leaving the last few posterior acrodont teeth in each jaw.

Acrodont teeth erupt posteriorly and are never shed. Erupting pleurodont teeth push out anterior acrodont teeth, but the final acrodont tooth count does not change once the animal has matured. Acrodont teeth undergo varying amounts of wear depending on age of the lizard and position of the tooth. Anteriormost acrodont teeth are abraded first by occlusion with their counterparts. In subadults the posterior quarter of the tooth row

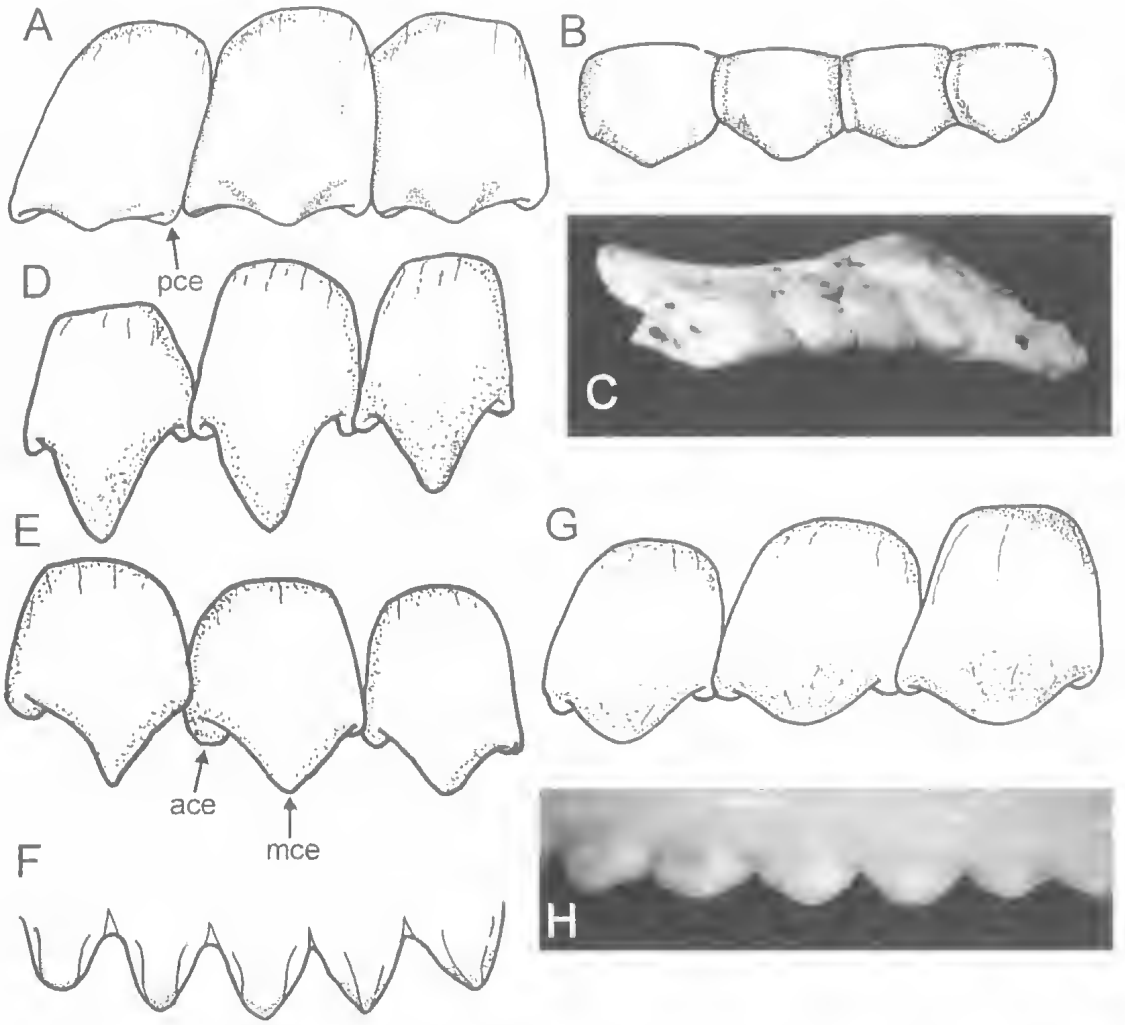

FIG. 1. Australian agamid maxillary acrodont tooth shapes. A, Quadrilateral-shaped (lingual view); B, Quadrilateral-shaped and socketed (labial view); C, Occlusal view; D, Mesocone dominant (lingual view); E, Antero-mesocone dominant (lingual view); F, Simple triangular (lingual view); G, Rounded (lingual view); H, Labial view. Abbreviations: pce; posterocone, ace; anterocone, mce; mescone.

usually has little or no wear. In old individuals wear may obliterate the entire acrodont and pleurodont tooth row, leaving a toothless ridge of jaw.

The acrodont tooth in most Australian agamids looks triangular after a period of wear. If a jaw has unworn teeth - generally the last 2-3 - then relative size, morphology and orientation of the cusps can be used for identification.

TOOTH TERMINOLOGY AND VARIATION

Pleurodont (P) and acrodont (A) teeth have their position along the tooth row indicated by a number in superscript for maxillary and subscript for dentary teeth. Acrodont teeth have 3 cusps variously expressed. To differentiate, the following terminology is used mirroring that for mammal teeth indicating upper and lower cusps: in the maxilla, the anterior cusp is the 'anterocone'; most prominent middle cusp is the 'mesocone'; and the posterior cusp is the 'posterocone'. In the dentary, the anterior cusp is the 'anteroconid'; middle, and most prominent, cusp the 'mesoconid'; and the posterior cusp the 'posteroconid' (Figs 1, 2).

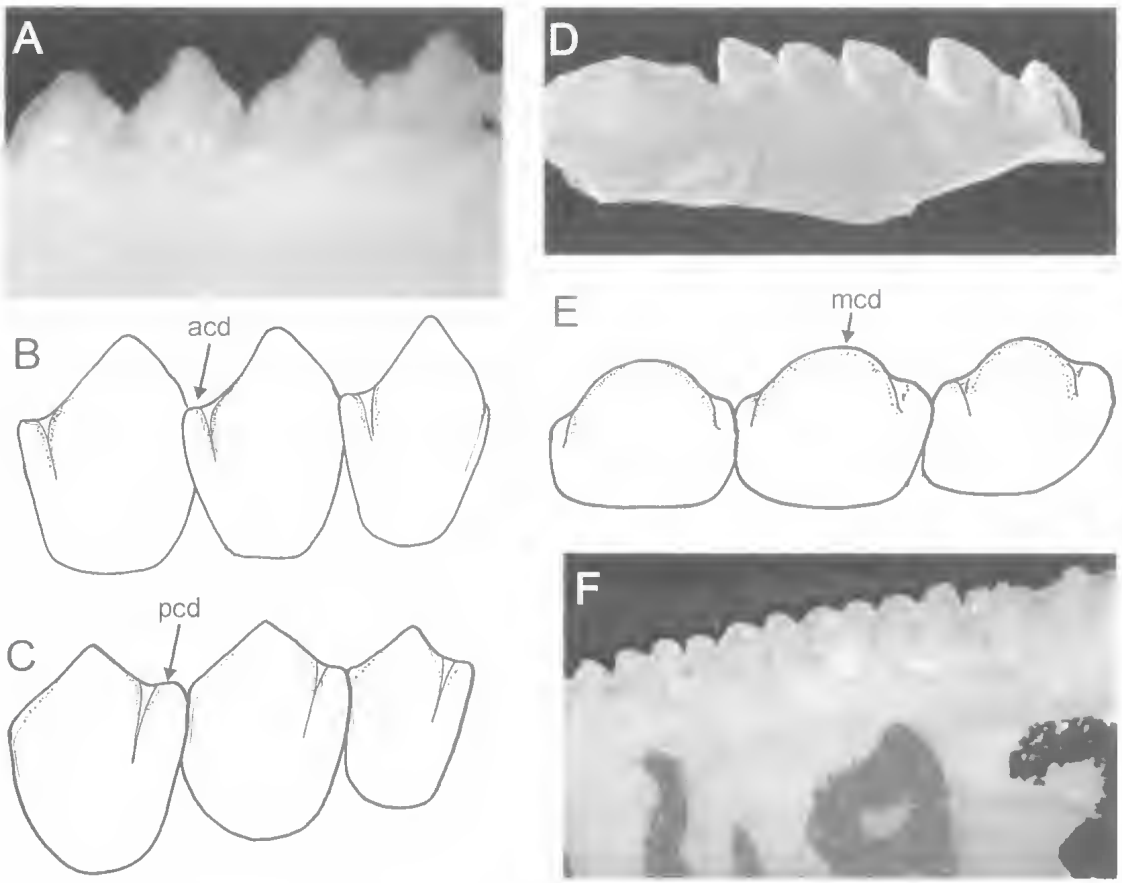

FIG. 2. Australian agamid dentary acrodont tooth shapes. A, Subtriangular (labial view); B, Anteroconid dominant (lingual view); C, Posteroconid dominant (lingual view); D, Reelined axis and crested (labial view); E, Rounded (lingual view); F, Tricuspid with labially displaced mesoconid (labial view). Abbreviations: acd; anteroconid, mcd; mesoconid, pcd; posteroconid.

Abbreviations. **acd**: anteroconid, **ace**: anterocone, **amh**: anterior maxillary height, **aml**: anterior maxillary length, **arl**: maxillary acrodont tooth row length, **darl**: dentary acrodont tooth row length, **dl**: dentary length, **dmk**: dorsal maxillary kink, **dmp**: dorsal maxillary process, **dmpw**: dorsal maxillary process width, **dms**: dorsal maxillary process slope, **ds**: dental sulcus, **ha**: hooked anterior margin, **ipmp**: inferior-posterior maxillary process, **jms**: jugal/maxillary suture, **lmf**: labial maxillary foramina, **mcd**: mesoconid, **mce**: mesocone, **mg**: Meckel's groove, **ml**: maxilla length, **n**: number of specimens, **pams**: palatine/maxillary suture, **pcd**: posteroconid, **pce**: posterocone, **pdd**: post- erior dentary depth, **pfms**: prefrontal/maxillary suture, **pms**: premaxillary/maxillary suture, **spmp**: superior-posterior maxillary process, **sym**: symphysis.

JUVENILES

Spirit juveniles show variations not present in any adult form: 1) A gradation of acrodont tooth size from smallest anteriorly to largest posteriorly, the posteriormost tooth being largest. In adults there is a marked division of acrodont tooth size into 'premolars' and 'molars', with most having the posteriormost tooth not the largest. 2) In juveniles sutures were not closed and the bone had not matured, so that bones were fragile and marginally translucent. In adults there is complete ossification and the bone is opaque. 3) Pleurodont teeth in juveniles are the same size as, or smaller than, the first acrodont tooth. After being replaced by the next pleurodont tooth generation, the lizard assumes the adult tooth size and size difference. 4) Juvenile acrodont teeth are hollow, compared with the robust, solid acrodont

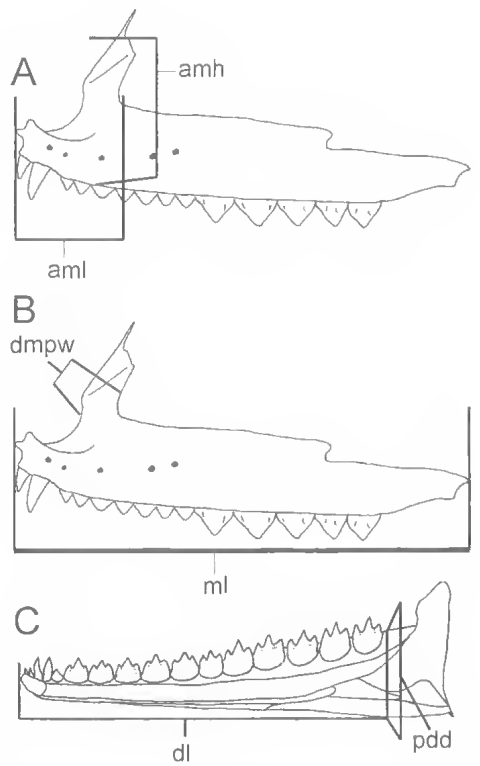

FIG. 3. Morphometric measurements taken for agamid maxillae and dentaries. A, B, Maxillary measurements; C, Dentary measurements.

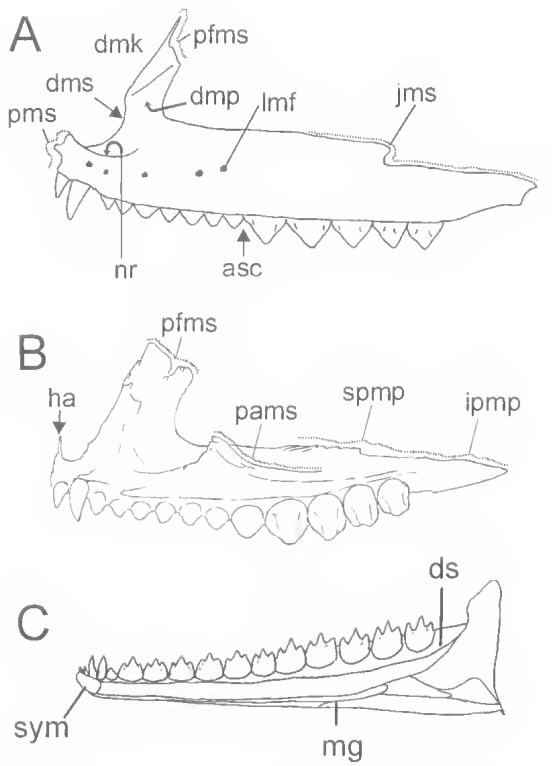

FIG. 4. Morphological features of the agamid maxillae and dentaries. A, B, Maxillary features; C, Dentary features.

teeth of adults. Sub-fossil juvenile agamid fragments from Henk's Cave, Lamington Plateau, *Physignathus lesueurii* and an unidentifiable specimen show the characters mentioned above.

SPECIES VARIATION

Adult Australian agamid genera belong to 3 size classes: large (total maxillary length - 18-50 mm, total dentary length - 22-50mm); medium (total maxillary length - 11-18mm, total dentary length - 14-20mm); and small (total maxillary length < 11mm, total dentary length < 14mm). Morphometric measurements used herein are illustrated in Fig. 3.

SEXUAL DIMORPHISM

Sexual dimorphism has not been prominent in species studied except for slight size differences. In the *Ctenophorus maculatus* and *C. pictus* species groups, and in *Tympanocryptis iutima* pleurodont teeth are larger in the males than in the females, but the overall morphology of the maxilla and acrodont tooth rows are similar.

SYSTEMATICS

Species not examined in the study are indicated by * in contents lists.

Family AGAMIDAE Gray, 1927

Amphibolurus Wagler, 1830

Amphibolurus is divided into two groups: Group 1 - *A. nobbi* and *A. muricatus*; Group 2 - *A. norrisi*.

Amphibolurus group 1 (Figs 5A-B, 9K)

Species included: *muricatus, nobbi nobbi, nobbi coggeri.*

Medium-sized.

MAXILLA. Pleurodont teeth 2, medium, unequal sized, closely set, straight, orientated medially; P^1, ¼ - ¾ the size of P^2. 13-14 acrodont teeth in *A. nobbi coggeri.* 16-17 quadrilateral acrodont teeth in *A.nobbi nobbi* and *A.muricatus.* Posteriormost acrodont teeth with antero- and posterocones. Naris ridge residual, only on the

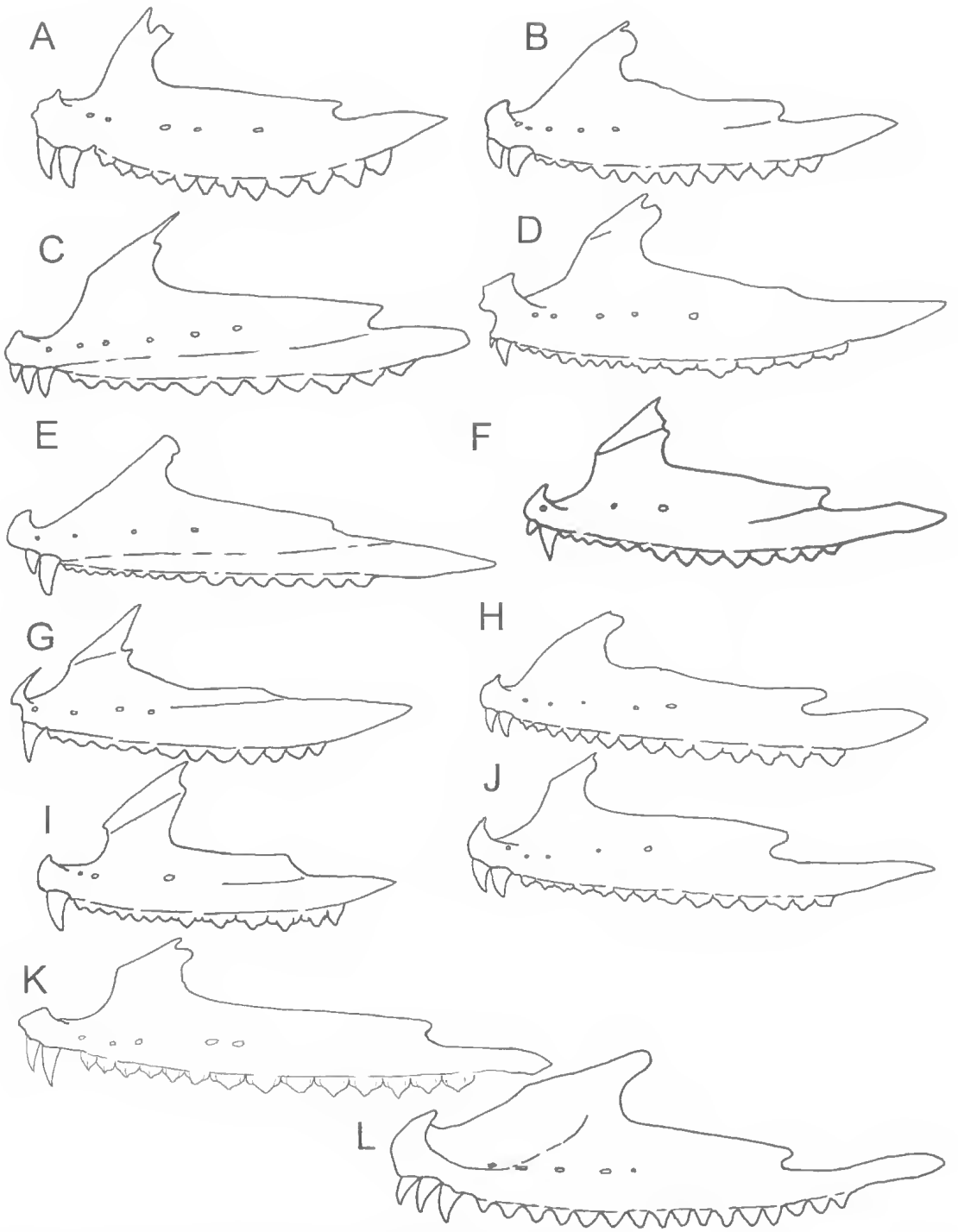

FIG. 5. Maxillae of the Australian agamids in labial view. A, *Amphibolurus muricatus*, x3.85; *B, Amphibolurus nobbi nobbi*, x3.90; C, *Amphibolurus norrisi,* x3.90; D, *Caimanops amphiboluroides*, x4.67; E, *Chlamydosaurus kingii*, x 1.90; F, *Diporiphora bennettii*, x5.63; G, *Diporiphora magna*, x3.76; H, *Lophognathus gilberti gilberti*, x3.3; I, *Diporiphora australis*, x4.0; J, *Lophognathus gilberti centralis*, x3.8; K, *Lophognathus temporalis*, x4.10; L, *Lophognathus longirostris,* x4.0.

anterolateral margin of the narial basin. Dorsal maxillary process slope, angular, approximately 30° from the longitudinal axis of the maxilla. Dorsal maxillary process slope mid-kink indistinct in *A. nobbi nobbi* and *A.muricatus*, yet conspicuous in *A.nobbi coggeri*. Broad dorsal maxillary process between the orbit and external naris. Anterior margin of the maxilla hooked distinctly. A diastema in front of P^1 with a distinct notch between P^1 and the premaxilla. Premaxillary/maxillary suture rounded anteriorly, orientated posterodorsally at its superior end. 3-4 maxillary foramina on labial side. Short and shallow jugal/maxillary suture.

DENTARY. Two, medium, unequally sized, anterolabially orientated pleurodont teeth in *A. nobbi nobbi* and *A. muricatus*. P_1, ¼ the size of P_2. One caniniform pleurodont tooth in *A.nobbi coggeri*. 16-17 subtriangular acrodont teeth in *A.nobbi nobbi* and *A. muricatus*. 14 subtriangular acrodont teeth in *A.nobbi coggeri*. Anterior end of the dentary narrow, tapering to a small triangular ovoid symphysis. Dentary gracile, long, for its height. 3-4 mental foramina.

REMARKS. *Amphibolurus* shares many features with *Diporiphora, Chlamydosaurus, Caimanops* and *Lophognathus* including: 1) angular dorsal maxillary process, 2) reduced or no naris ridge, 3) a notch anterior to P^1 and 4) long, gracile dentaries. *Amphibolurus* is distinguished from *Diporiphora* by its much larger size and 2 equally sized maxillary pleurodont teeth, instead of either a singular caniniform pleurodont tooth, or a P^1, which is much smaller and orientated anterolabially to the P^2. *A. nobbi coggeri* shares a single large caniniform dentary pleurodont tooth with *Diporiphora*, however, it can be distinguished by being larger and its reduced antero- and posteroconids. *Amphibolurus* is markedly smaller than *Chlamydosaurus* and *Lophognathus* with fewer acrodont teeth and smaller pleurodont teeth. *Amphibolurus* is similar in maxillary length to *Caimanops* but differs by possessing larger, spaced pleurodont, and longer anterior acrodont teeth. *Caimanops has* a more distinct notch anterior of the P^1. When comparing the ratio of acrodont tooth row length to the number of acrodont teeth, *Amphibolurus* falls within the range of *Lophognathus*, is larger than *Diporiphora* and *Caimanops*, but much smaller than *Chlamydosaurus*.

Amphibolurus group 2 (Fig. 5C)

Species included: *norrisi*

Medium-sized.

MAXILLA. Pleurodont teeth 3, large, recurved, unequally sized, closely spaced, orientated medially, produced labially from the midline of the acrodont tooth arcade. P^1, ½ the size of $P^{2\&3}$. P^2 equal in size to P^3. A distinct notch in front of the first pleurodont tooth, producing a short diastema between P^1 the last premaxillary pleurodont tooth. 6-7 maxillary foramina on the labial side. Premaxillary/maxillary suture rounded, orientated posterodorsally at its superior margin. Naris ridge inconspicuous, reduced to the anterior margin of the premaxillary/maxillary suture. Dorsal maxillary process angular, at approximately 30° from the longitudinal axis of the maxilla. Slight kink in the midline of the dorsal maxillary process. Dorsal maxillary process very broad. 13-14 acrodont quadrilateral-shaped teeth. Jugal/maxillary suture long, deep. Maxillary flexure negligible.

DENTARY. Long, gracile, tapering sharply from posterior to anterior. Two, medium-sized, unequal sized, anterolabially orientated pleurodont teeth. P^1, ½ the size of P^2. 15-16 simple conical acrodont teeth with reduced antero- and posteroconids. Meckelian groove parallel to dental sulcus in the anterior half of the dentary. Dental sulcus abruptly angled dorsal two-thirds the way down the jaw line. 5-6 mental foramina.

REMARKS. *A. norrisi* has the longest maxillae and dentaries of any *Amphibolurus*, 3 large maxillary pleurodont teeth, reduced antero- and posteroconids. The naris ridge is almost absent, whereas it is only reduced in *A. nobbi* and *A. muricatus*. The dorsal maxillary process is broader in *A. norrisi* than in *A. muricatus* and *A. nobbi*.

Caimanops Storr, 1974 (Fig. 5D)

Species included: *amphiboluroides*

Medium-sized.

MAXILLA. Two, unequal, medially orientated pleurodont teeth with P^1, ½ the size of P^2. P^2 recurved. Naris ridge at base of the anterior margin of the narial basin. 4-5 maxillary foramina on the labial side. Dorsal maxillary process slope approximately 45° from the longitudinal axis of the maxilla, with a kink midway up the slope. A distinctly notched diastema between P^1 and the premaxilla. Premaxillary/maxillary suture elaborate,

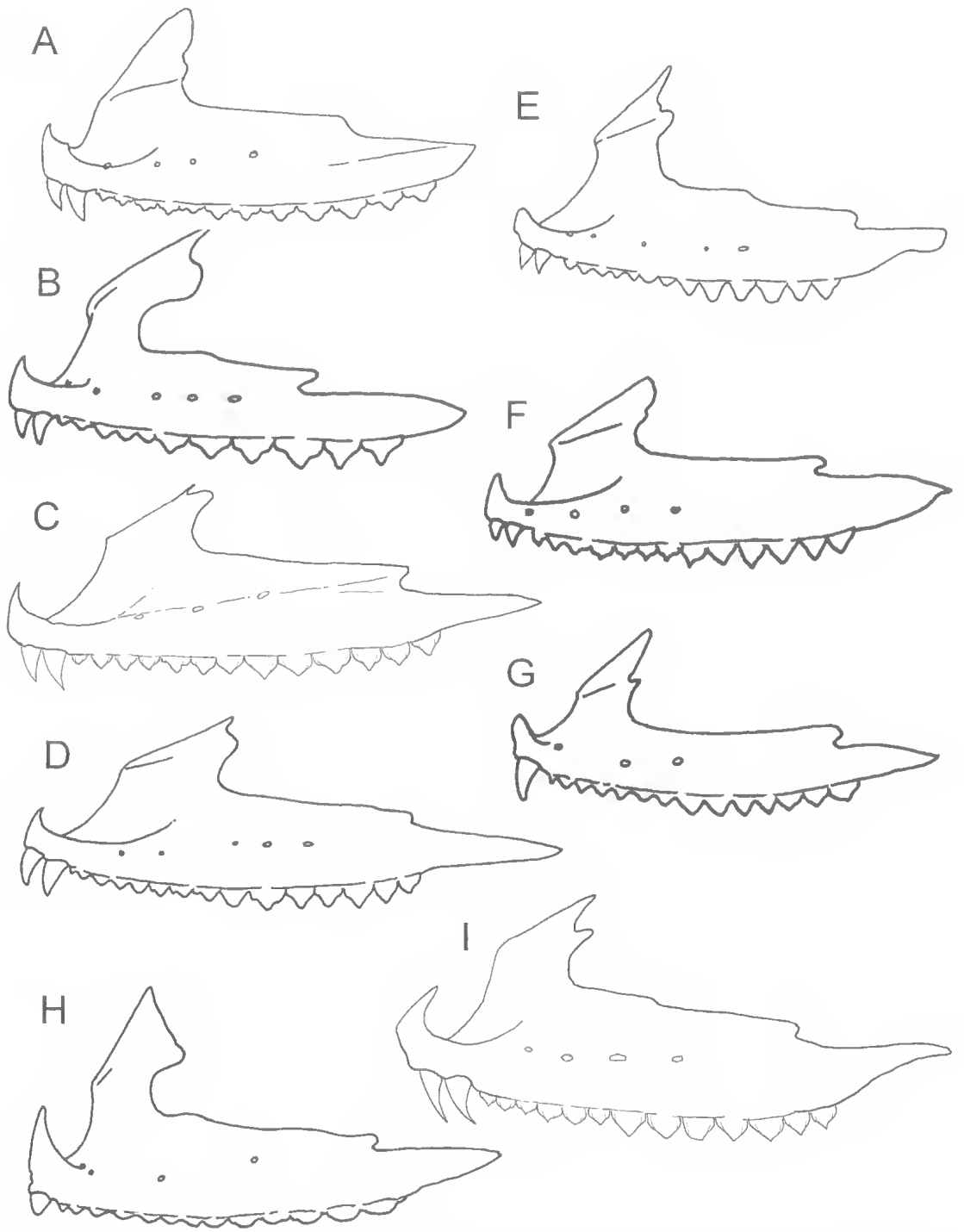

FIG. 6. Maxillae of the Australian agamids in labial view. A, *Ctenophorus candicinctus*, x5.2; B, *Ctenophorus cristatus*, x4.64; C, *Ctenophorus decresii*, x5.85; D, *Ctenophorus ornatus* x5.6; E, *Ctenophorus maculatus*, x6.3; F, *Ctenophorus isolepis*, x6.8; G, *Ctenophorus pictus*, x5.54; H, *Ctenophorus nuchalis*, x4.6; I, *Ctenophorus scutulatus*, x4.84.

sigmoid-shaped in lateral profile. Dorsal maxillary process broad. 16 mesocone dominant acrodont teeth with equally sized antero- and posterocones half the size of the mesocone. Jugal/maxillary suture long and shallow.

DENTARY. Two pleurodont teeth with P_1 ½ the size of P_2. P_2 caniniform. Both pleurodont teeth labially orientated. 17 subtriangular acrodont teeth compressed laterally, of equal size along the dental arcade, broad at their bases. Posteroconid larger than anteroconid. Jaw narrow, tapering abruptly anteriorly. Meckel's groove parallel to the dental sulcus.

REMARKS. *Caimanops* is similar in size to *Amphibolurus*, but has smaller pleurodont and acrodont dentition and a better developed posteroconid. The premaxillary/maxillary notch is also more pronounced in *Caimanops*. *Caimanops* is larger than *Diporiphora* and has smaller pleurodont teeth. *Caimanops* is smaller then *Lophognathus* and is considerably smaller in the pleurodont and acrodont teeth. *Caimanops* is most similar to *Chlamydosaurus*, having an equally prominent premaxillary/maxillary notch, similar pleurodont tooth size difference and general shape of the anterior margin of the maxilla. The second dentary pleurodont tooth of *Caimanops* is large and caniniform, which is markedly similar to the single caniniform dentary pleurodont tooth found in *Chlamydosaurus*. *Caimanops* differs from *Chlamydosaurus* by being much smaller and its more elaborate premaxillary/maxillary suture.

Chelosania Gray, 1845 (Fig. 8D)

Species included: *brunnea*

Medium-sized.

MAXILLA. Pleurodont teeth 1-2, equal, small, similar in size to A^1, straight, medially orientated. 14-15 acrodont teeth within one dental arcade, with each tooth similar in size along the tooth row. Posteriormost acrodont teeth with distinct postero- and anterocones, anterocones approximately half height of mesocone. Mesocone tip rounded. 5-6 maxillary foramina on the labial side. Naris ridge extending inferior to the narial basin, ending 3/4 the way up the dorsal maxillary process (near complete). Dorsal maxillary process equally broad along its height, being one of the broadest dorsal maxillary processes for any endemic Australian agamid. Dorsal maxillary process with breadth comparable to *Physignathus*. Dorsal maxillary process slope steep, at approximately 60°, curving posteriorly at its dorsal margin. Premaxillary/maxillary suture begins immediately in front of P^1, curving anterodorsally to the premaxilla. This produces a distinctly hooked anterior margin of the maxilla. Jugal/maxillary suture short and deep.

DENTARY. Stout, deep posteriorly. Pleurodont tooth small, medially orientated, equal in size to A^1. Acrodont teeth 14-15, tricuspid. Postero- and anteroconids equal. Meckel's groove not parallel to the dental sulcus. Subdental bone above the Meckel's groove deep. 3-4 mental foramina.

REMARKS. *Chelosania* bears very few features in common with endemic Australian agamids except *Physignathus lesueurii*, to which it is very similar in many aspects of the skull and jaws. *Chelosania* is also strikingly similar to *Hydrosaurus*, *Physignathus cocincinus* and *Hypsilurus bruynii* from PNG. These features include, a broad dorsal maxillary process and complete naris ridge, which are considered symplesiomorphic. *Chelosania* shares a distinct anteroconid with *Lophognathus gilberti*, *Lophognathus temporalis* and *Caimanops*.

Chlamydosaurus Gray, 1825 (Figs 5E, 9P)

Species included: *kingii*

One of the largest Australian agamids.

MAXILLA. Pleurodont teeth 2, very large, recurved, caniniform, labially orientated, set labially to the acrodont tooth row, with P^2 2-3 times larger than P^1 and recurved labially. A notch in front of P^1, producing a diastema between the maxilla and the premaxilla. Premaxillary/maxillary suture rounded, angled posteriorly at its dorsal margin, producing a distinctly hooked anterior margin to the maxilla. Naris ridge residual. Dorsal maxillary process slope angled at approximately 45°, with no midline kink. 5-6 maxillary foramina on the labial side of the maxilla. Jugal/maxillary suture long, deep. Broad dorsal maxillary process constricted dorsally. Acrodont teeth 17-18, within a single arcade, of similar size with a single large mesocone.

DENTARY. Long, narrow, tapering sharply posteriorly. Pleurodont tooth large, caniniform, recurved, anterolabially orientated. Acrodont teeth 19-20, conical, monocuspid. Symphysis large, ovoid. Meckel's groove not parallel to the dental sulcus. 4-5 mental foramina.

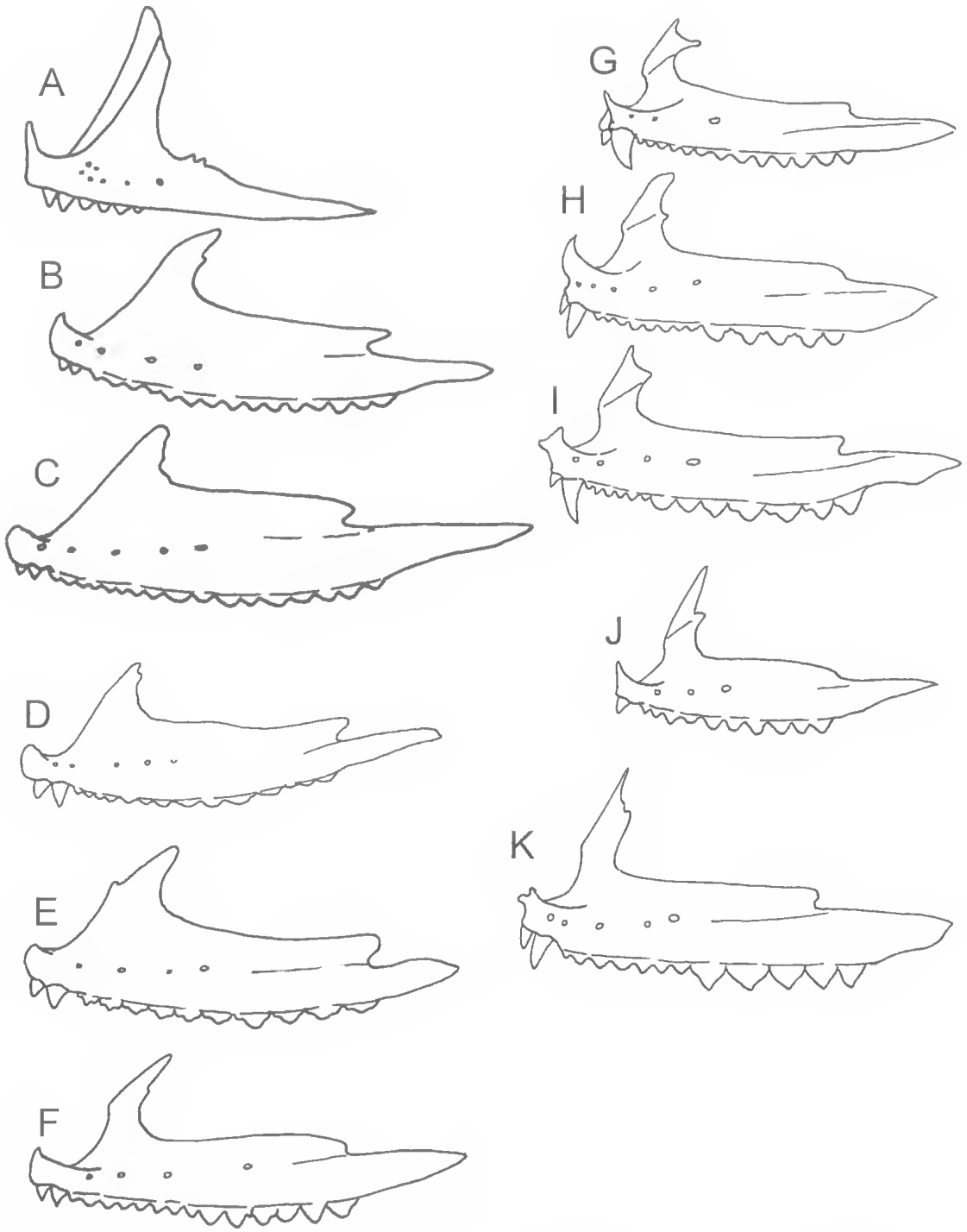

FIG. 7. Maxillae of the Australian agamids in labial view. A, *Moloch horridus,* x5.6; B, *Pogona barbata,* x.55; C, *Pogona vitticeps,* x1.80; D, *Pogona mitchelli,* x2.4; E, *Pogona minor,* x3.15; F, *Rankinia diemensis,* x6.3; G, *Tympanocryptis intima,* x5.2; H, *Tympanocryptis cephalus,* x 5.4; I, *Tympanocryptis tetraporophora,* x6.1; J, *Tympanocryptis parviceps,* x5.1; K, *Tympanocryptis lineata,* x6.2.

REMARKS. *Chlamydosaurus* is the largest of a group comprising *Amphibolurus*, *Diporiphora*, *Caimanops* and *Lophognathus*. It dwarfs all four genera in overall maxillary, dentary and dentition dimensions. It differs from *Amphibolurus* and *Lophognathus* in its unequal maxillary pleurodont teeth and a single caniniform dentary pleurodont tooth. *Chlamydosaurus* differs from *Diporiphora* by its more distinct premaxillary/maxillary notch. *Chlamydosaurus* is most similar to *Caimanops*, from which it only differs significantly in being much larger and having a less complex premaxillary/ maxillary suture.

Ctenophorus Fitzinger, 1843

Ctenophorus consists of 8 species groups (Wilson & Knowles, 1988) some of which contain only a single species, but many subspecies. To capture the greatest amount of osteological variation, the present study has taken representatives from all of the species groups used by Wilson & Knowles (1988).

Ctenophorus caudicinctus (Figs 2A, 6A, 9H)

Species included: *caudicinctus*.

Medium-sized; consists of several distinct subspecies (Wilson & Knowles, 1988).

MAXILLA. Pleurodont teeth 2, large, spaced, recurved, unequal, orientated labially. P^1, ½ the size of P^2. Naris ridge distinct, bordering the narial basin and up the dorsal maxillary process, half the way. Dorsal maxillary process slope with a distinct kink in the midline. Dorsal maxillary process slope orientated at approximately 45° to the longitudinal axis of the maxilla. Dorsal maxillary process moderately broad. 3-4 maxillary foramina on the labial side, with distinctly hooked anterior end. Acrodont teeth 13-14, mesocone dominant, with small antero- and posterocones. Narial foramen on the dorsal maxillary process. Jugal/maxillary suture short, deep.

Dentary. Pleurodont teeth 2, small, unequal; P_1 small, orientated anterolabially, ½ the size of P_2. P_2 medium-sized, caniniform, orientated labially. Acrodont teeth 14-15, simple, monocuspid. Mental foramina 3-4.

REMARKS. This species group differs from the *ornatus* species group by its fewer acrodont teeth and a less developed superior process of the posterior margin of the maxilla; from the *decresii* species group by having spaced maxillary pleurodont teeth and a better-developed naris ridge; from the *maculatus* species group by its markedly larger maxilla and acrodont tooth; from the *scutulatus* species group by being smaller with fewer acrodont teeth; and from all other species of *Ctenophorus* by its broader and lower dorsal maxillary process, which is not vertical, a better developed naris ridge and a distinct diastema between P^1 of the maxilla and the premaxillary/maxillary suture.

Ctenophorus cristatus (Figs 1D, 6B)

Species included: *cristatus*

Medium-sized. Contains several subspecies.

MAXILLA. Pleurodont teeth 2, medium, equal, recurved, spaced, labially orientated. Premaxillary/maxillary suture curving dorsally, immediately anterior to P^1, then hooking posterodorsally to the nasals. Narial foramen on the dorsal maxillary process slope. Dorsal maxillary process slope near vertical, with distinct midline kink. A ridge running posterolaterally from this kink to the maxillary/prefrontal suture. Naris ridge moderately developed, bordering the narial basin. Maxillary foramina 4-6, on the labial side. Jugal/maxillary suture deep and long. Superior maxillary process long, producing a tongue-shaped process on the jugal. Acrodont teeth 11-13, mesocone dominant, with small postero- and anterocones.

DENTARY. Pleurodont teeth 2, small, equal, orientated anterolabially. Acrodont teeth 12-14, subtriangular, with simple conical mesoconids and diminutive, equally sized antero- and posteroconids. Meckel's groove parallel to the dental sulcus. Mental foramina 3-4.

REMARKS. *C cristatus* species group differs from the *pictus* species group by possessing 2 medium-sized, instead of 1 large maxillary pleurodont teeth, by being smaller and having greater ratio of acrodont tooth row length to acrodont tooth count (0.84-0.90 vs. 0.62-0.72).

C. cristatus species group differs from the *reticulatus* species group by possessing a less right-angled dorsal maxillary process relative to the longitudinal axis of the maxilla, larger maxillary and dentary pleurodont teeth and greater ratio of acrodont tooth row length to acrodont tooth count (0.84-0.90 vs. 0.60-0.78).

The *C. cristatus* species group differs considerably from the remaining *Ctenophorus* species groups by its narrower dorsal maxillary

process, higher dorsal maxillary process, smaller maxillary pleurodont teeth, more reduced naris ridge and a more vertically oriented dorsal maxillary process relative to the longitudinal axis of the maxilla.

Ctenophorus decresii species group (Fig 6C)

Species included: *decresii*, *fionni*, *rufescens*.

Medium-sized.

MAXILLA. Pleurodont teeth 1-2, large, closely spaced, recurved, equal, orientated labially. Naris ridge distinct, running the border of the narial basin and up the dorsal maxillary process, half of the way. Dorsal maxillary process with a distinct mid-kink. Dorsal maxillary proeess slope orientated at approximately 45° to the longitudinal axis of the maxilla. Dorsal maxillary process broadened inferiorly, constricted superiorly. Maxillary foramina 4-5 on the labial side. Distinctly hooked anterior margin with a diastema anterior to P^1. Acrodont teeth 13-14, simple, with small but distinct antero- and posterocones. Narial foramen on the dorsal maxillary process. Jugal/maxillary suture short and deep.

DENTARY. Pleurodont teeth 2, small, unequal; P_1 small, ½ the size of P_2, orientated anterolabially. P_2 medium-sized, caniniform, orientated labially. Acrodont teeth 14-15. Mental foramina 4-5.

REMARKS. The *C. decresii* species group has spaced maxillary pleurodont teeth and a better developed naris ridge than *C. caudicinctus*. *C. decresii* has a deeper subnaris ridge zone and less developed naris ridge than the *C. scutulatus group*. The *C. ornatus* species group is very similar to the *C.decresii* species group differing only in size.

The C.decresii differs from the other members of *Ctenophorus* by possessing a broader dorsal maxillary process, better-developed naris ridge, larger pleurodont dentition, by being larger and having less angular dorsal maxillary process in relation to the longitudinal axis of the maxilla. *C.rufescens* is only the second *Ctenophorus* species observed with one large, caniniform maxillary pleurodont tooth. The anterior margin of the maxilla is very similar to other members of the species group, which is in turn considerably different to *C. pictus* - the only other *Ctenophorus* with a single large caniniform pleurodont tooth.

Ctenophorus ornatus species group (Fig. 6D)

Species included: *C. ornatus*, **C. yinnietharra*.

Medium-sized.

MAXILLA. Pleurodont teeth 2, oriented labially, large, spaced, recurved, equal. Naris ridge distinct, running the border of the narial basin and up the dorsal maxillary process slope half of the way. Dorsal maxillary process with a distinct kink in the midline. Dorsal maxillary process slope orientated at approximately 45° from the longitudinal axis of the maxilla. Dorsal maxillary process constricted superiorly, broadening to the inferior margin. Maxillary foramina 4-5, on the labial side. Distinctly hooked anterior margin. Acrodont teeth 12-13, mesocone dominant, with equally sized antero and posterocones. Narial foramen at the base of the dorsal maxillary process. Jugal/maxillary suture short, shallow.

DENTARY. Pleurodont teeth 2, unequal; P_1 small, ½ the size of P_2, orientated anterolabially; P_2 medium-sized, caniniform, orientated labially. Acrodont teeth 14-15, simple, subtriangular. Meckel's groove of uniform depth, parallel to the dental sulcus. Mental foramina 4-5.

REMARKS. The *C. ornatus* species group differs from the *C.scutulatus* species group by possessing a lower dorsal maxillary process and less labial maxillary pleurodont dentition; from the *C. decresii* species group by being smaller; from the *C.caudicinctus* species group by possessing a lower dorsal maxillary process and a less developed superior process of the posterior margin of the maxilla; from the *C. maculatus* species group by its larger maxillary and dentary pleurodont and acrodont teeth its lack of maxillary flexure and its larger size; from the remaining *Ctenophorus* species groups by its broader, lower and less vertical dorsal maxillary process, larger maxillary pleurodont teeth and better developed naris ridge.

Ctenophorus maculatus species group (Figs 6E-F, 9E)

Species included: *maculatus, isolepis, femoralis, *fordi, *rubens*

Small.

MAXILLA. Pleurodont teeth 2, medium-sized, equal, recurved, oriented medially. Diastema between P^1 and premaxilla. Anterior margin of the maxilla distinctly hooked, producing the premaxillary/maxillary suture. Superior margin

of the premaxillary/maxillary suture orientated posterodorsally. Naris ridge borders the narial basin, ending halfway up the dorsal maxillary process. Narial foramen on the dorsal maxillary process slope. Dorsal maxillary process slope oriented near vertical but with a midline kink. Dorsal maxillary process moderately broad relative to maxillary length. Maxillary foramina 3-4, on labial side of the maxilla. Jugal/maxillary suture, long, shallow. Acrodont teeth 12-13, mesocone dominant, with tapered antero- and posterocones. Maxillary flexure present.

Dentary. Pleurodont teeth 2, unequal, anterolabially orientated, with P_1, ½ the size of P_2. Acrodont teeth 12-13, subtriangular. Meckel's groove parallel to the dental sulcus. Jaw line elongate, shallow. Mental foramina 3-4.

REMARKS. The *C. maculatus* species group have sexually dimorphic skull. Males in each observed species have larger and more recurved pleurodont dentition than females.

Although much smaller, the *C.maculatus* species group is similar to the *C.ornatus* and *C.caudicinctus* species groups, but it differs from the *C. ornatus* species group by its maxillary flexure, smaller acrodont and pleurodont teeth in the maxilla and dentary and lower ratio of acrodont tooth row length to acrodont tooth count (0.51-0.62 vs 0.77); from the *C.caudicinctus* species group by its smaller and fewer acrodont teeth, less maxillary flexure and lower ratio of acrodont tooth row length to acrodont tooth count (0.51-0.62 vs. 0.60 - 0.74); and from other *Ctenophorus* species groups by its broader dorsal maxillary process, smaller acrodont teeth and distinctly flexed maxilla,

Ctenophorus pictus (Figs 6G, 9F)

Species included: *Ctenophorus pictus*

Medium-sized.

MAXILLA. Pleurodont tooth 1, large, recurved, caniniform, labially orientated. Acrodont teeth 12-13, mesocone dominant, with diminutive antero- and posterocones. Maxillary foramina 4-5. Long and shallow jugal/maxillary suture. Premaxillary/maxillary suture distinct, originating immediately in front of a notch anterior to the pleurodont tooth, orientated anterodorsally. Medially, the suture bends posterodorsally. Dorsal maxillary process slope orientated at greater than 60° to the longitudinal axis of the maxilla, with a midline kink. Dorsal maxillary process broad inferiorly, constricted superiorly. Naris ridge bordering the narial basin, ending just posterior of this. Superior process of posterior maxillary margin simple, gently curved.

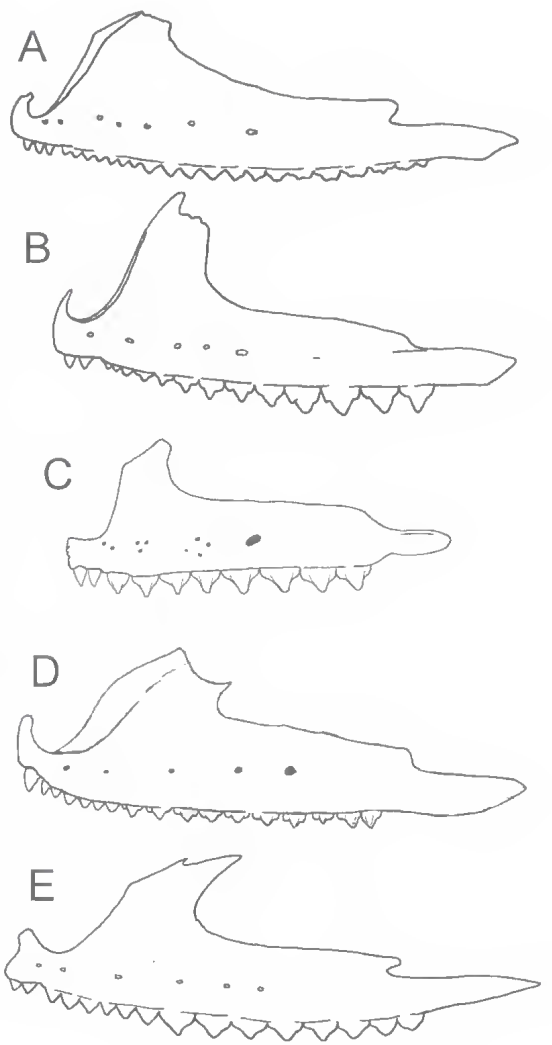

FIG. 8. Maxillae of the Australian agamids in labial view. A, *Physignathus lesueurii*, x1.5; B, *Physignathus lesueurii*, subadult, x2.0; C, *Physignathus lesueurii*, juvenile, x3.8; D, *Chelosania brunnea*, x4.2; E, *Hypsilurus spinipes*, x2.8.

DENTARY. Shallow. Pleurodont tooth 1, large, caniniform, recurved, anterolabially orientated. Acrodont teeth 13-14, subtriangular, laterally compressed. Dental sulcus running parallel to the

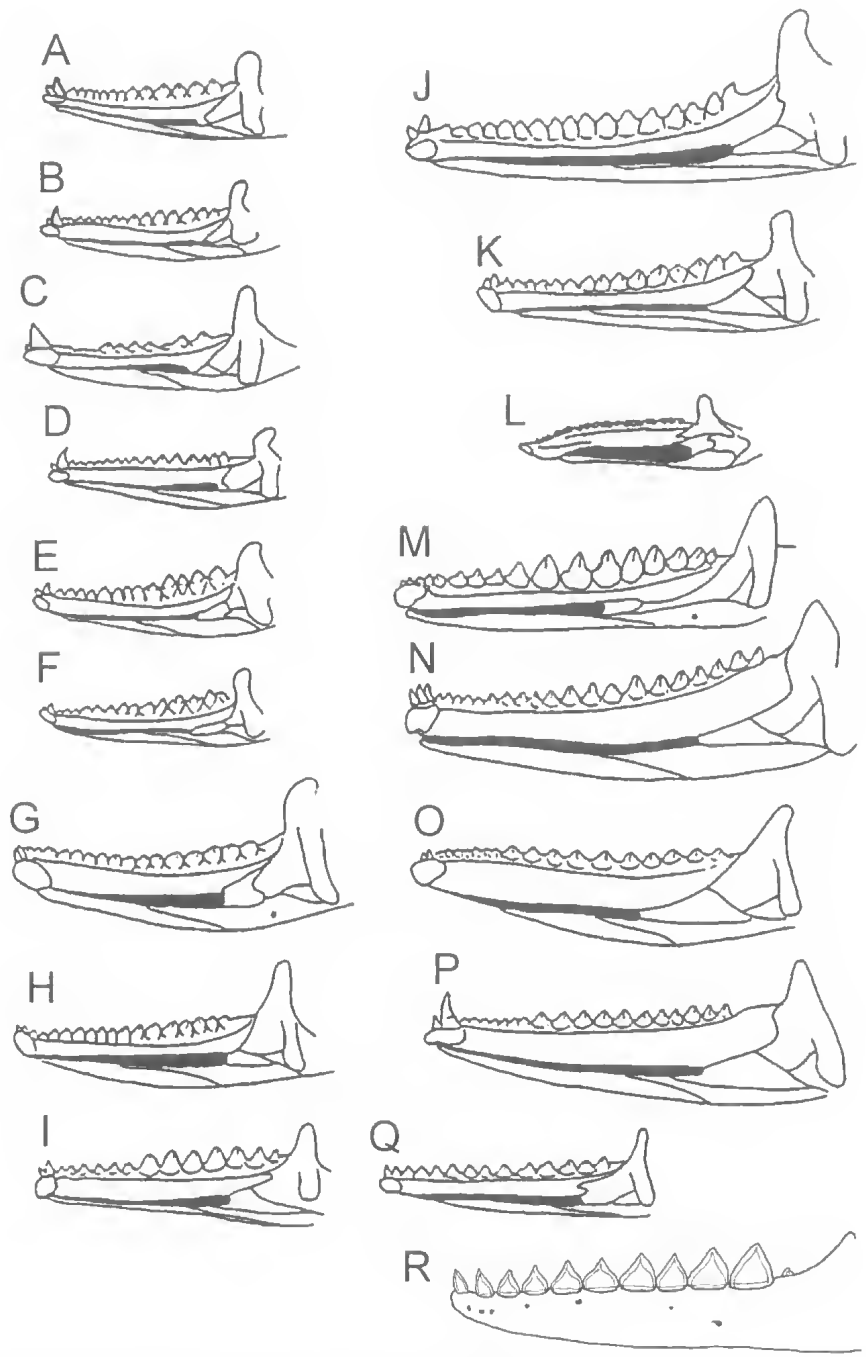

FIG. 9. A selection of Australian agamid dentaries in lingual view. A, *Tympanocryptis lineata*, x2.0; B, *Tympanocryptis cephalus*, x2.0; C, *Tympanocryptis intima*, x2.0; D, *Tympanocryptis tetraporophora*, x2.0; E, *Ctenophorus isolepis*, x2.0; F, *Ctenophorus pictus*, x2.0; G, *Ctenophorus nuchalis*, x2.0; H, *Ctenophorus caudicinctus*, x1.3; I, *Rankinia diemensis*, x3.0; J, *Lophognathus longirostris*, x1.6; K, *Amphibolurus nobbi*, x1.75; L, *Moloch horridus*, x2.0; M, *Hypsilurus spinipes*, x1.5; N, *Physignathus lesueurii*, x1.0; O, *Pogona barbata*, x1.3; P, *Chlamydosaurus kingii*, x1.2; Q, *Diporiphora australis*, x2.0; R, *Physignathus lesueurii*, juvenile, x6.0.

Meckel's groove. Symphysis small, ovoid. Mental foramina 3-4. Narial foramen on the dorsal maxillary process.

REMARKS. This species group exhibits sexual dimorphism with male maxillary and dentary pleurodont teeth being larger and more caniniform than females. It is distinct within the genus by its singular, large, caniniform maxillary and dentary pleurodont dentition. The anterior margin of the maxilla is similar to the *C. cristatus* species group, including the breadth, height and angle of the dorsal maxillary process, development of the naris ridge, and number and size of acrodont teeth.

Ctenophorus reticulatus species group
(Figs 6H, 9G)

Species included: *Ctenophorus reticulatus*, *Ctenophorus nuchalis* and *Ctenophorus maculosus*.

Medium and small-sized.

MAXILLA. Pleurodont teeth 1-2, equal, small, orientated meso-labially, equal to or slightly larger than A^1. Acrodont teeth 12-15, rounded, labiolingually expanded. Premaxillary/maxillary suture beginning directly anterior to P^1, with the anterior margin directed vertically to suture with the premaxilla. Naris ridge reduced to border the first portion of the narial basin. Narial foramen on the dorsal maxillary process. Dorsal maxillary process slope near vertical, with reduced or no midline kink. Dorsal maxillary process narrow. Jugal/maxillary suture short, shallow. Maxillary foramina 4-5, on the labial side.

DENTARY. Deep, stout. Pleurodont teeth 1-2, small, equal, labially orientated, same size or slightly larger than A_1. Acrodont teeth 12-15, rounded, conical in labial profile. Mental foramina 4-5. Meckel's groove broad, not parallel to dental sulcus. Dental sulcus curving dorsally immediately below the last three acrodont teeth.

REMARKS. *C. reticulatus* and *C. nuchalis* are the most similar species. *C.maculosus* differs from *C. reticulatus* and *C. nuchalis* by being smaller, having fewer acrodont teeth, its 2 (not 1) maxillary pleurodont teeth, one large caniniform dentary pleurodont tooth and better developed naris ridge.

The *C. reticulatus* species group differs from the *C .cristatus* species group by its narrower dorsal maxillary process orientated more vertically, smaller maxillary pleurodont teeth, a less developed naris ridge and a lower ratio of acrodont tooth row length to acrodont tooth count; and from the remaining species of *Ctenophorus* by its narrow dorsal maxillary process, vertically orientated dorsal maxillary process, residual naris ridge and smaller maxillary and dentary pleurodont teeth.

The *C.reticulatus* species group resembles *Pogona* in the narrow dorsal maxillary process, reduced naris ridge, rounded, labiolingually expanded, maxillary and dentary acrodont dentition, small pleurodont teeth equal in size to A^1 and A_1, but differs in its more vertical dorsal maxillary process, smaller size and smaller acrodont tooth row length to acrodont tooth count ratio.

Ctenophorus scutulatus species group
(Fig. 6I)

Species included: *scutulatus*, **mckenziei*.

Medium-sized. One of largest groups in *Ctenophorus*.

MAXILLA. Pleurodont teeth 2, large, closely spaced, recurved, equal, orientated labially at approximately 20° to the sagittal axis of the maxilla. Naris ridge distinct, running the border of the narial basin and halfway up the dorsal maxillary process slope. Dorsal maxillary process broad, with a distinct kink in the midline. Dorsal maxillary process slope orientated at approximately 45° to the longitudinal axis of the maxilla. Maxillary foramina 5-6, on the labial side. Distinctly vertical and posterodorsal orientation of the premaxillary/maxillary suture. Acrodont teeth 13-14, mesocone dominant, with small tapered antero- and postcrocones. Narial foramen on the dorsal maxillary process. Jugal/maxillary suture long, shallow.

DENTARY. Long, gracile. Pleurodont teeth 2, small, unequal; P_1 small, orientated anterolabially, ¼ the size of P_2; P_2 medium-sized, orientated labially. Acrodont teeth 14-15, subtriangular. Mental foramina 3-4. Symphysis small, ovoid.

REMARKS. The *C. scutulatus* species group does not differ substantially from the *C. decresii* and *C. ornatus* species groups, but differs from all other *Ctenophorus* species by its larger size, better developed naris ridge, broad and angular dorsal maxillary process.

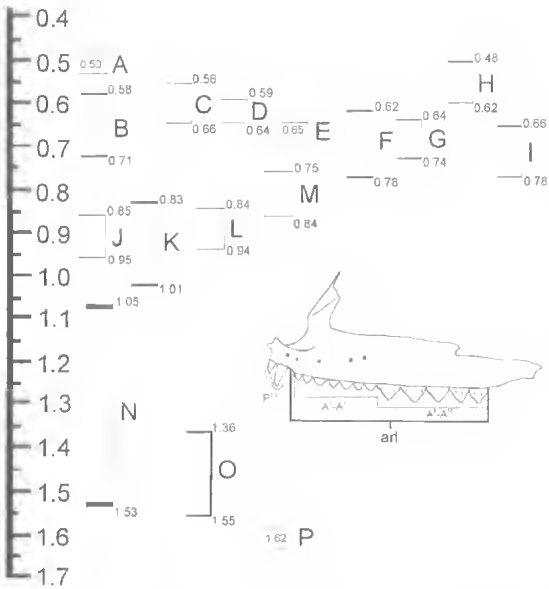

FIG. 10. Maxillary acrodont tooth row length (arl) to acrodont tooth row count for Australian agamid genera. Single figures are mean values for monotypic genera. Range values given for polytypic genera. A, *Moloch*; B, *Diporiphora*; C, *Tympanocryptis*; D, *Rankinia*; E, *Caimanops*; F, *Ctenophorus pictus*; G, *Ctenophorus caudicinctus*; H, *Ctenophorus maculatus* species group; I, *Ctenophorus reticulatus* species group; J, *Amphibolurus*; K, *Lophognathus*; L, *Ctenophorus cristatus*; M, *Ctenophorus decresii* and *Ctenophorus ornatus* species groups combined. N, *Pogona*; O, *Physignathus*; P, *Chlamydosaurus*.

Diporiphora Gray, 1842

Diporiphora is divided into two groups based on the number of maxillary pleurodont teeth. Species not available in this study are *D. convergens, D. linga, D. reginae* and *D. valens*.

Diporiphora group 1 (Fig. 5F)

Species included: *D. bennettii, D. albilabris.*

Medium-sized.

MAXILLA. Pleurodont teeth 2, with P^1 ½ the size of P^2; P^2 large, caniniform, recurved, oriented mesolabially. P^1 small, recurved, orientated anteromedially. Acrodont teeth 13-14, monocuspid, subtriangular. Maxillary foramina 3, on the labial side. Naris ridge residual. Dorsal maxillary process low, constricted superiorly, broadened inferiorly. Premaxillary/maxillary suture anterodorsal to P^1, orientated posterodorsally. Suture gracile. Acrodont teeth mesocone dominant, with equally sized antero- and posterocones. Jugal/maxillary suture short, relatively deep. Moderate amount of maxillary flex.

DENTARY. Pleurodont teeth 2; P_1 small, orientated anterolabial; P_2 large, caniniform, orientated anterolabially. Acrodont teeth 15-16, subtriangular, with moderately developed posteroconids in the last five teeth. Meckel's groove parallel with the dental sulcus. Symphysis small, ovoid. Mental foramina 5.

REMARKS. Group 1 is the smaller *Diporiphora* species group and differs from group 2 by its 2 maxillary pleurodont teeth, instead of a singular caniniform maxillary pleurodont tooth. *Chlamydosaurus* is the only genus that shares such a massive caniniform dentary pleurodont tooth. *Diporiphora* group 1 differs from *Chlamydosaurus* by being considerably smaller and possessing 4-5 fewer acrodont teeth.

Diporiphora group 2 (Figs 2C, 5G, I, 9Q)

Species included: *D. winneckei, D. magna, D. australis, D. bilineata, D. pindan*

Medium-sized.

MAXILLA. Pleurodont tooth 1, large, recurved, mesolabially orientated, caniniform, labial to the longitudinal maxilliary axis. Notch in front of the pleurodont tooth, with the premaxillary/ maxillary suture beginning directly above this notch. Suture running dorsally, then reoriented posteriorly. Naris ridge residual. Dorsal maxillary process relatively broad. Dorsal maxillary process slope steep, approximately 60° from the longitudinal axis of the maxilla at its base. Midway up the dorsal maxillary slope it is directed posteriorly at 45°. Acrodont teeth 14-15, mesocone dominant, with little development of antero- or posterocones. Jugal/maxillary suture long, shallow. Maxillary foramina 4.

DENTARY. Pleurodont teeth 2, caniniform, mesolabially orientated, with P_1 very small and P_2 large. Meckel's groove not parallel to the dental sulcus. Symphysis large, ovoid. Acrodont teeth 14, subtriangular, with better developed posteroconid. Mental foramina 4.

REMARKS. Group 2 differs from Group 1 by its singular caniniform maxillary pleurodont tooth.

Lophognathus Gray, 1842

REMARKS. *Lophognathus* is the second largest genus within the group with *Chlamydosaurus*, *Amphibolurus*, *Diporiphora* and *Caimanops*. *Lophognathus*, except *L. longirostris*, is most similar to *Amphibolurus*, but differs in being larger, possessing more prominent maxillary pleurodont teeth, more distinct anterocones, and a broader dorsal maxillary process

Lophognathus group 1 (Figs 1E, 2B, 5H-K)

Species content: *Lophognathus gilberti gilberti*, *L. gilberti centralis*, *L. temporalis*.

Large.

MAXILLA. Pleurodont teeth 2, large, near equal, recurved, closely set, labial to the acrodont tooth row. Naris ridge residual. Dorsal maxillary process slope approximately 45° to the longitudinal axis of the maxilla. Dorsal maxillary process broad, without mid kink. Maxillary foramina 4-5, on the labial side. Premaxillary/maxillary suture rounded, originating directly anterior to P^1. Anterior region including the premaxillary/maxillary suture hooked prominently posterodorsally. Diastema between P^1 and the premaxilla absent. Jugal/maxillary suture long, deep. Acrodont teeth 15, quadrilateral; posterior-most teeth with conspicuous anterocones and sometimes a well-developed posterocone.

DENTARY. Pleurodont teeth 2, labially orientated; P_1 much smaller than P_2, P_2 caniniform, recurved. Symphysis small, ovoid. Acrodont teeth 15-16, antero/mesoconid dominant. Jaw long and gracile in lateral profile. Meckel's' groove parallel to the dental sulcus. Mental foramina 3-4.

REMARKS. Group 1 differs from Group 2 by having fewer pleurodont and simpler acrodont teeth.

Lophognathus group 2 (Figs 5L, 9J)

Species included: *Lophognathus longirostris*

This is the largest species of *Lophognathus*.

MAXILLA. Pleurodont teeth 2-3, large, recurved, spaced, set labially away from the acrodont tooth line; P^1 orientated anterolabially, $^2/_3$ the size of P^2; P^2 orientated mesolabially, equal to P^3; P^3 orientated posterolabially. Naris ridge extending to midway up dorsal maxillary process. Dorsal maxillary process slope angled below 45° from the longitudinal axis of the maxilla. Notch anterior to P^1 absent. Premaxillary/maxillary suture rounded, beginning from immediately anterior to P^1. Jugal/maxillary suture short and deep. Maxillary foramina 4-5, on the labial side. Acrodont teeth 16-17, quadrilateral.

DENTARY. Long, narrow. Pleurodont teeth 2-3, unequal, orientated anterolabially; P_1, ½ the size of P_2. Where present, P_2 and P_3 are equal. Acrodont teeth 18-19, subtriangular, with no development of the antero- and posteroconids. Meckel's groove parallel to dental sulcus. Symphysis small, ovoid. Mental foramina 4-5.

REMARKS. *L. longirostris* is distinct within the genus on its high pleurodont and acrodont tooth count, a broad dorsal maxillary process with a distinct and well-developed naris ridge and its dentary acrodont teeth with indistinct antero- and posteroconids.

Moloch Gray, 1841 (Figs 1F, 2F, 7A, 9L)

Species included: *Moloch horridus*

Small.

MAXILLA. Pleurodont teeth 2-3, equal, small, approximately equal to A^1. Acrodont teeth 15, orientated lingually at approximately 80° to the longitudinal axis of the maxilla, triangular, with a single mesocone, without antero- and posterocones, wear produces the crowns into a sculptured crescentric shape. Naris ridge complete, running the length of the dorsal maxillary process. A diastema between P^1 and the premaxilla. Premaxillary/maxillary suture curved anterodorsally, produced by a thin anterior spike of the maxilla. Jugal/maxillary suture without a superior posterior maxillary process, therefore has no distinguishable depth, long, running from the palatine/maxillary suture to the posterior margin of the posterior maxillary process. Dorsal maxillary process near vertical, narrow in lateral view, broad in anterior view, expanded laterally to be a broad partition between orbit and naris. Labial maxillary foramina 6-7.

DENTARY. Pleurodont teeth 2-3, small, equal, spaced, similar in size to A_1. Acrodont teeth 15-16, with antero- and posteroconids orientated dorsoventrally along the longitudinal axis, with mesoconid orientated labiolingually to the longitudinal line, with anterocristid developed into a posterolabially directed lophid, with

osterocristid developed into an anterolabially directed lophid. Meckel's groove very wide, with a heavily reduced dental sulcus. Symphysis tiny, oval. Mental foramina 5-6.

REMARKS. This taxon shares no close maxillary or dentary characters with any other Australian agamid. Although *Moloch* is highly derived for a small-sized dragon, it has a near complete naris ridge, high maxillary foramina count and a high maxillary pleurodont count.

Physignathus Cuvier, 1829
(Figs 1A, 8A-C, 9N, R)

Species included: *Physignathus lesueurii, Physignathus cocincinus.*

Large.

MAXILLA. Pleurodont teeth 3, medium-sized, equal, labially orientated, straight. Premaxillary/maxillary suture beginning directly anterior to the first pleurodont tooth, producing a hooked anterior margin of the maxilla. Dorsal maxillary process broad. Naris ridge complete, originating near the premaxillary/maxillary suture, terminating beneath the nasal bone, anterior to the maxillary/prefrontal suture. Narial basin deep. Maxillary foramina 6-7, on labial side. Jugal/maxillary suture short, deep. Acrodont teeth 18-19, quadrilateral, with well-developed equal antero and posterocones half the size of the mesocone. Dorsal maxillary process slope steep, approximately 60° from the longitudinal axis of the maxilla.

DENTARY. Deep, stout. Pleurodont teeth 3, medium-sized, equal, orientated anterolabially. Acrodont teeth 18, with a slightly developed anteroconid. Meckel's groove broad, beginning anterior to the last 4-5 acrodont teeth. Mental foramina 5-6.

REMARKS. *Physignathus* shares with *Chelosania* a distinct naris ridge, broad dorsal maxillary process, and a deep, stout dentary, but differs by being much larger and possessing a greater number of pleurodont and acrodont teeth.

Pogona Storr, 1982
(Figs 1G-H, 2E, 7B-E, 9O)

Species content: *barbata, vitticeps, minor, mitchelli, nullabor, * henrylawsoni.*

Pogona is a medium-sized to large-sized agamid genus. *Pogona henrylawsoni* is the smallest of the group, however, it was not available for this study.

MAXILLA. Pleurodont teeth 2, small to medium-sized, unequal in small species (*minor, mitchelli, nullabor*) with P^1 orientated anterolabially to P^2, equal in large species (*vitticeps, barbata*) with $P^{1\&2}$ approximately the same size or slightly larger than A^1. Acrodont teeth 11-17, rounded, with conspicuously rounded cones. Maxillary foramina 3-4, on the labial side. Mesocone expanded labiolingually. Dorsal maxillary process steep, approximately 60° from the longitudinal axis of the acrodont tooth row, narrow superiorly, broad basally. Jugal/maxillary suture long, deep. Naris ridge residual. Premaxillary/maxillary suture rounded, continuous with the premaxilla. Anterior margin of the maxilla hooked slightly.

DENTARY. Stout, robust, deep in larger species. Pleurodont teeth 2, small to medium-sized; in large species small, equal, similar in size to A^1; in small species medium-sized, orientated anterolabially for P_1 and mesolabially for P_2. P_1, ½ the size of P_2. Acrodont teeth 13-20, rounded, conical in lateral profile. Mental foramina 4-5.

REMARKS. *Pogona* shares with the *Ctenophorus reticulatus* species group a high and near vertical dorsal maxillary process, rounded acrodont dentition, deep posterior margin of the dentary and small equally sized pleurodont teeth (in the larger species) but differs by being much larger (with the possible exception of *Pog. henrylawsoni*), having broader dorsal maxillary processes inferiorly, larger and more acrodont teeth and greater acrodont tooth length to acrodont tooth number ratio (1.06-1.53 vs. 0.6-0.78).

Rankinia Wells & Wellington, 1985
(Figs 7F, 9I)

Species included: *R. diemensis, R. adelaidensis, R. chapmani*

Small.

MAXILLA. Pleurodont teeth 2-3, small, equal, closely set, orientated meso-labially. Acrodont teeth 11-13, subtriangular, with distinct, equally sized antero- and posterocones. Mesocone very large, at least twice the size of the antero- and posterocones. Naris ridge reduced. Dorsal maxillary process narrow, near vertical. Premaxillary/maxillary suture rounded, continuous with the line of the pleurodont teeth.

A small diastema occurs directly anterior to P^1. Maxillary foramina 3-5. Jugal maxillary suture long, shallow. Narial foramen at the base of the dorsal maxillary process.

DENTARY. Long, gracile, with rounded anterior, with very small symphysis. Pleurodont teeth 2, small, spaced, equal, straight, mesolabially orientated. Acrodont teeth 14, subtriangular, with reduced antero- and posterocones. Mental foramina 4-5.

REMARKS. *Rankinia* is most similar to *Tympanocryptis* and the *Ctenophorus reticulatus* species group with its constricted, near vertical dorsal maxillary process, reduced naris ridge and small size, but it differs from the *C. reticulatus* species group by having shallower maxillae and dentaries and from *Tympanocryptis* by the lack of caniniform pleurodont teeth in both the maxilla and dentary.

Tympanocryptis Peters, 1863
(Figs 7G-K, 9A-D)

Species included: *intima, cephalus, "lineata", tetraporophora, parviceps, *uniformis.*

Small.

MAXILLA. Pleurodont teeth 2; P^2 caniniform, oriented mesolabially, twice the size of P^1; P^1 oriented either anterolabial (*tetraporophora, intima*) or mesolabial (*"lineata", cephalus*). Acrodont teeth 12-13, mesocone dominant, with equal antero- and posterocones. Premaxillary/maxillary suture directly anterodorsal of the pleurodont teeth, high above the tooth row with a distinct mid-length notch, continuing dorsally, produced by the hooked anterior margin of the maxilla. Dorsal maxillary process narrow. Naris ridge reduced to border the length of the narial basin. Narial foramen on the labial edge of the narial basin. Dorsal maxillary process slope near vertical. Foramina 3-5, on the labial side. Jugal/maxillary suture long, beginning above the last 4-5 acrodont teeth.

DENTARY. Short, stout. Pleurodont teeth 2, closely spaced, anterolabially orientated; P_1 ½ the size of P_2; P_2 large, caniniform. Acrodont teeth 13-14, subtriangular, with indistinct antero- and posteroconids. Dental sulcus narrow, running the entire length of the dentary. Meckel's groove parallel to dental sulcus. Meckelian groove narrowed anteriorly, sometimes closed in *T. intima*. Mental foramina 2-3.

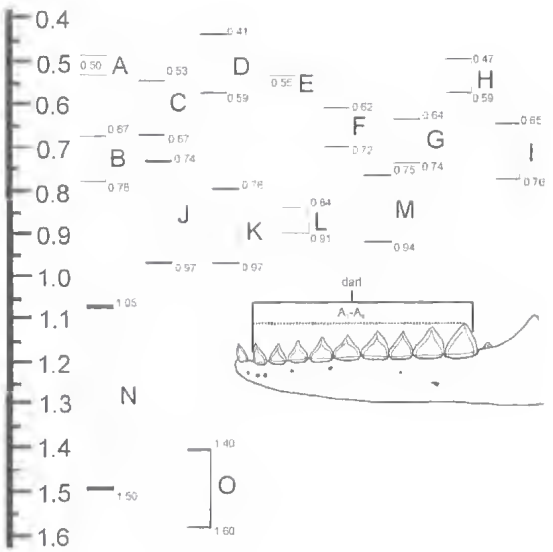

FIG. 11. Dentary acrodont tooth row length (darl) to acrodont tooth row count for Australian agamid genera. Single figures are mean values for monotypic genera. Range values given for polytypic genera. A, *Moloch*; B, *Diporiphora*; C, *Tympanocryptis*; D, *Rankinia*; E, *Caimanops*; F, *Ctenophorus pictus*; G, *Ctenophorus caudicinctus*; H, *Ctenophorus maculatus* species group; I, *Ctenophorus reticulatus* species group; J, *Amphibolurus*; K, *Lophognathus*; L, *Ctenophorus cristatus*; M, *Ctenophorus decresii* and *Ctenophorus ornatus* species groups combined; N, *Pogona*; O, *Physignathus*; P, *Chlamydosaurus*

REMARKS. *Tympanocryptis* is easily distinguished from all other Australian agamids by the shape of the anterior maxillary margin, shape of the premaxillary/maxillary suture, very large caniniform P2 on both maxillary and dentary and constricted, near vertical dorsal maxillary process.

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APPENDIX 1

SKULL COMPARATIVE MATERIAL LIST

Agama stellio: MNHN1991.4020, *Amphibolurus muricatus*; QMJ1042, AMR-unregistered, AMR1480, *Amphibolurus nobbi nobbi*; QMJ38748, *Amphibolurus nobbi coggeri*; SAMR13162, *Amphibolurus norrisii*; WAMR unregistered, *Caimanops amphiboluroides;* WAMR14464, *Calotes critellatus*; MNHN 1991.4002, *Chelosania brunnea;* NTR8700, NTR9924, *Chlamydosaurus kingii*; QMJ3718, QMJ5707, QMJ19707, QMJ21929, QMJ47642, *Ctenophorus candicinctus*; QMJ21654, SAMR03467, SAMR29492, WAMR82712, WAMR47832, WAMR47833, NTR1557, NTR11115, *Ctenophorus clayi*; WAMR71343, *Ctenophorus cristatus*; SAMR3026, SAMR3029, SAMR20771, WAMR47841, WAMR101474, NTR1096,

NTR9208, *Ctenophorus decresii*: AMR81641, SAMR9382, SAMR9385, NTR6956 *Ctenophorus femoralis*; WAMR47835, *Ctenophorus fionni*; QMJ274, SAMR9230, SAMR10105, SAMR13320, SAMR13899, NTR8263, *Ctenophorus fordi*; QMJ50835, QMJ22734, *Ctenophorus isolepis*: (juvenile) QMJ48488, QMJ24824, SAMR5303, SAMR15517B, SAMR15517F, NTR20437, NTR31418, *Ctenophorus maculatus*; WAMR14021, *Ctenophorus maculosus*: SAMR unregistered X 2, *Ctenophorus nuchalis*; QMJ705, SAMR7304, SAMR7309, WAMR28140, WAMR47837, WAMR82656, WAMR113073, NTR18496, NTR18819, NTR31447, NTR31541, *Ctenophorus ornatus*; WAMR30073, *Ctenophorus pictus*: QMJ48074, SAMR741, SAMR8952, SAMR14479, SAMR19249, SAMR26561, WAMR66973, NTR17428, NTR18497, *Ctenophorus reticulatus*; SAMR29252, WAMR47834, 93129, *Diporiphora albilabris*: NTR1232, NTR4101, *Diporiphora australis*; QMJ44926, QMJ29907, *Diporiphora bennetti*; NTR9490, NTR32541, *Diporiphora bilineata*; QMJ11141, QMJ44926, *Diporiphora lalliae*, NTR286 NTR1514 *Diporiphora magna*; NTR3685, NTR22619, *Diporiphora winneckei*; NTR11133, NTR15099, *Guntacephalus grandis* WAMR49516, UMMZR170383, *Hydrosaurus pustulatus*, UMMMZR188050, UMMZR188058, *Hypsilurus boydii*; QMJ17799, QMJ1002, *Hypsilurus spinipes*; QMJ8330, QMJ42424, QMJ45306, *Lophognathus gilberti*; QMJ39042, NTR33496, NTR33499, *Lophognathus longirostris*; QMJ61729, NTR15248, NTR33570, NTR10867, *Lophognathus temporalis*; QMJ46374, NTR6184, NTR22947, *Moloch horridus*; QMJ11492, SAMR22514, *Physignathus cocincinus*: MNHN1991.4259-60, *Physignathus lesueurii*: QMJ5449, QMJ26671, QMJ38108, QMJ43834, QMJ47973, *Pogona barbata*: QMJ14402, QMJ23950, QMJ47070, QMJ47077, QMJ57296, *Pogona minor*; NTR31429, SAMR587, SAMR14857, *Pogona mitchelli*, NTR10576, NTR31430, *Pogona nullabor*, SAMR18581,

Pogona vitticeps: QMJ37168, QMJ37167, *Rankinia adelaidensis*, WAMR9831, *Rankinia diemensis*: AMR70141, WAMR9830, *Tympanocryptis cephalus*: QMJ21659, NTR16767, NTR16768, *Tympanocryptis intima*: QMJ47889, SAMR14422, SAMR15323, *Tympanocryptis lineata*; QMJ8604, NTR18746, NTR23209, *Tympanocryptis tetraporophora*: QMJ34580, SAMR16599, *Uromastyx acanthinura*: MNHN 1991.4265-57.

APPENDIX 2

Key to modern Australian agamid genera using the maxilla.

1. Naris ridge present 2
   Naris ridge absent, or residual 3
2. Naris ridge complete (or near complete) 4
   Naris ridge ends posterior to the narial basin, on the dorsal maxillary process 5
   Naris ridge borders narial basin 6
3. Dorsal maxillary process broad . . . . . *Hypsilurus*
   Dorsal maxillary process constricted superiorly and broad inferiorly 7
4. One pleurodont tooth and a broad dorsal maxillary process . . . . . *Chelosania*
   Two or usually three pleurodont teeth 8
5. One, large, caniniform pleurodont tooth . . . . . *Ctenophorus pictus* or *Ctenophorus rufescens*
   Two, equal, large, pleurodont teeth . . . . . *Ctenophorus ornatus*, *Ctenophorus decresii*, *Ctenophorus caudicinctus* and *Ctenophorus scutulatus* sp. groups.
   Two, equal small, to medium-sized pleurodont teeth . . . . . *Ctenophorus maculatus* sp. group
   Three, spaced, recurved pleurodont teeth. . . . . *Lophognathus longirostris*
6. Two, equal pleurodont teeth 9
   Two, unequally sized pleurodont teeth with the second caniniform, with a distinct notch anterodorsal to P1 . . . . . *Tympanocryptis*
7. One, large, caniniform tooth. . . . *Diporiphora* sp group 1
   Two, P^2 at least twice the size of P^1 10
   Two, P^1 approximately ¾ or equal to P^2 12
   Three large pleurodont teeth . . . *Amphibolurus norrisi*
8. Acrodont teeth orientated parallel to the longitudinal axis of the maxilla. . . . . *Physignathus*
   Acrodont teeth orientated lingually at approximately 90° from vertical axis of maxilla . . . . . *Moloch*
9. Narial foramen on dorsal maxillary process. 11
   Narial foramen within narial basin. Very long jugal/maxillary suture. . . . . *Rankinia*
10. Premaxillary/maxillary suture distinctly ornate, sigmoid-shaped. Total maxillary length less than 18mm . . . . . *Ctenomops*
    Premaxillary/maxillary suture simple, rounded suture. Total maxillary length greater than 30mm . . . . . *Chlamydosaurus*
    Premaxillary/maxillary suture simple, rounded suture. Total maxillary length less than 15mm . . . . . *Diporiphora* group 2
11. Acrodont teeth with rounded crowns, with equally sized antero- and posterocones . . . . . *Ctenophorus reticulatus* species group
    Acrodont teeth with mesocone dominant, with tooth crowns not distinctly rounded . *Ctenophorus cristatus*
12. Acrodont teeth quadrilateral. 13
    Acrodont teeth with rounded crowns, with equally sized antero- and posterocones . . . . . *Pogona*
    (only applicable if dentary dentition is known)
13. Anteroconid distinct, posteroconid reduced or absent . . . . . *Lophognathus*
    Both antero- and posteroconids reduced. . . . . *Amphibolurus nobbi*/*A. muricatus*.